3. Woodlots as Biogeographic Islands in Southeastern Wisconsin

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The concepts of island biogeography have been broadly tested with data on invertebrates (Wilson and Simberloff 1969, Simberloff and Wilson 1969, 1970), mammals (Crowell 1973), and birds (Diamond 1969, 1973, Terborgh and Faaborg 1973). Plant communities on islands have also been examined in Puerto Rico (Heatwole and Levins 1973), in Lake George, New York (Slack et al. 1975), and in Lake Mockeln, Sweden (Nilsson 1978). For terrestrial "habitat islands," i.e., small patches of habitat in a regional landscape, Vuilleumier (1970), Brown (1971), and Picton (1979) related species richness to "island" size and isolation after examining the bird and mammal populations of mountaintops. Culver (1970a) utilized the concepts to consider the biota of caves, while Janzen (1968) compared individual host plants to islands in time and space for the individual insects that feed on them.

Kolata (1974), Diamond (1975a), Sullivan and Shaffer (1975), and Goeden (1979) all have suggested using island biogeographic concepts as the basis for establishing a network of wildlife preserves. On a smaller scale, the same basic concepts have been applied to county parks and rural woodlots (Forman and Elfstrom 1975, Galli et al. 1976, Whitcomb 1977, Gottfried 1979). Extension to woodlots and parks of urban systems seems to be an appropriate application of the habitat island concept (Davis and Glick 1978).

In the metropolitan Milwaukee, Wisconsin area, major alterations of the landscape pattern such as the addition or deletion of islands, resulting in changes in interisland distances and matrix qualities, are caused by human activity. In the process, the rates of colonization and extinction are continually altered. In natural communities, succession is a mechanism for such change. However, successional patterns resulting from urban influences may differ from those expected under natural conditions.

In this chapter, we consider the parks and woodlots in metropolitan Milwaukee as biogeographic islands in order to examine the applicability of the concepts of island biogeography to isolated woodlots in an agro-urban matrix. Specific objectives were (1) to survey and assess the forest plant communities that are embedded and isolated from each other in nonforest matrix; (2) to test the applicability of the concepts of island biogeography that relate island size to species richness of the forested "habitat island"; and (3) to provide concepts useful for regional landscape planning and resource management.

Description of the Study Area

The study area was metropolitan Milwaukee, an area of about 525 km^2, including Milwaukee County, southern Ozaukee County, and the eastern portions of Waukesha and Washington Counties (Fig. 3-1).

Climate

The region has a continental climate, modified by Lake Michigan. Average monthly temperatures range from -6.2°C in January to 21.5°C in July. Average annual precipitation is about 76.2 cm with nearly two-thirds falling during the frost-free season.

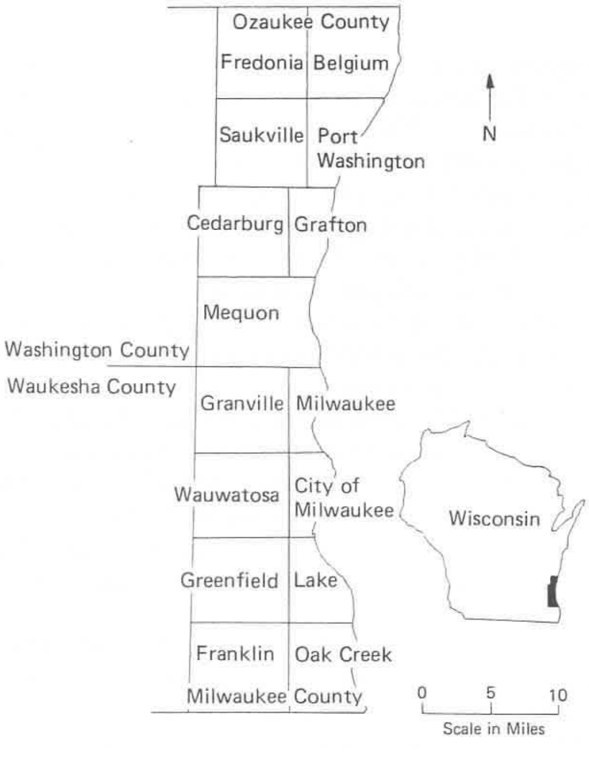


Fig. 3-1. Map showing the distribution of civil townships in Milwaukee and Ozaukee counties, Wisconsin.

Areas adjacent to the lake are generally cooler in the summer and warmer in the winter than more westerly locations. The average length of the growing season near Lake Michigan in Milwaukee County is 180 days, but drops to less than 160 days within 50 km to the northwest (Fig. 3-2).

Physiography and Soils

Glacial features dominate the landscape. Two to three undulating moraines with intervening troughs parallel the Lake Michigan shoreline (Fig. 3-3). Drainage, poorly integrated and controlled by the moraines, is largely confined to the troughs that harbor the Milwaukee, Root, and Menomonee Rivers (Fenneman 1938, Thornbury 1965). Generally, local relief is slight, but the northwestern portion of the study area is characterized by kettle and kame topography.

The pattern of soil associations in southeastern Wisconsin (Fig. 3-3) is closely correlated with glacial features, primarily the end moraines and adjacent ground moraines. Ozaukee-Morley-Mequon soils occupy morainic uplands, accounting for about 80% of the study area. The Ozaukee and Morley soils (Typic Hapludalfs) are well drained to moderately well drained and are characterized by moderately slow permeability and moderate fertility. The Mequon series (Udollic Ochraqualf) consists of somewhat poorly

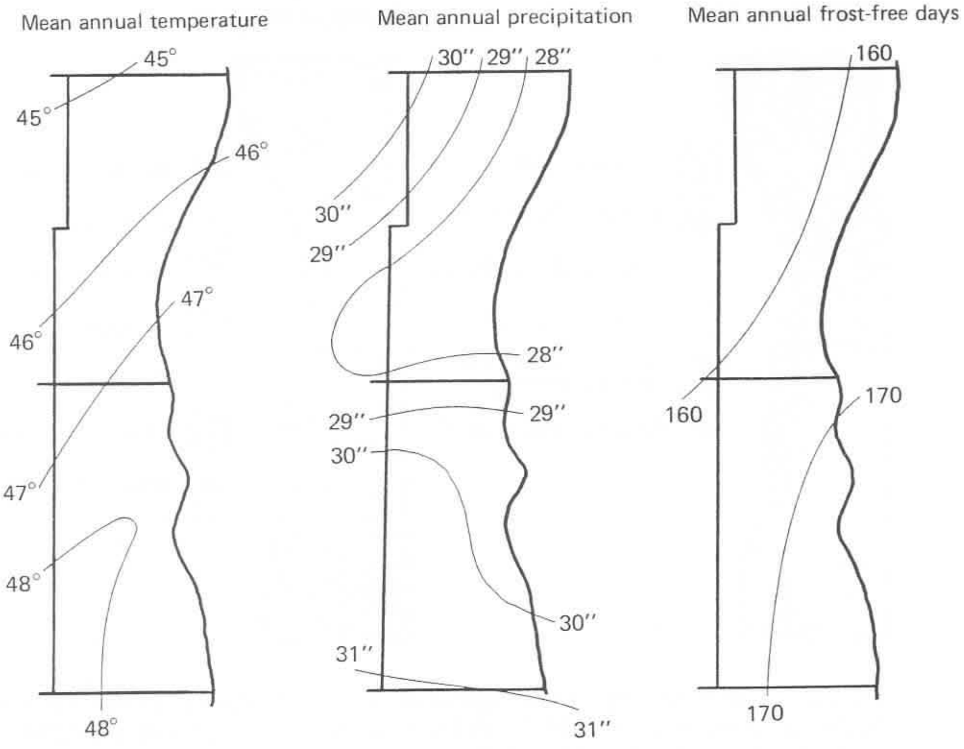
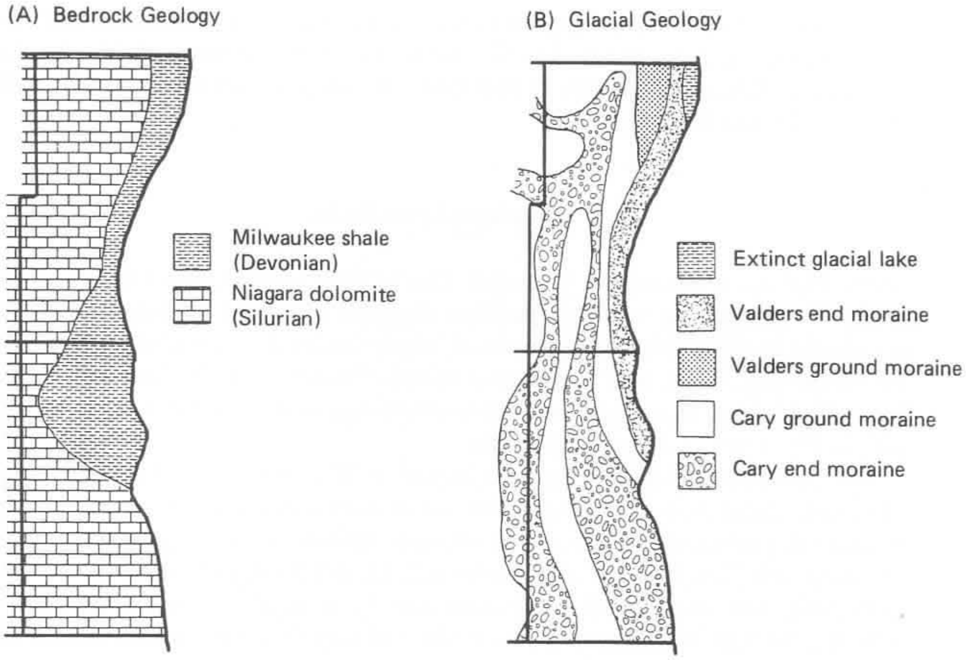


Fig. 3-2. Climatic summary of the metropolitan Milwaukee region (redrawn from SEWRPC 1963).



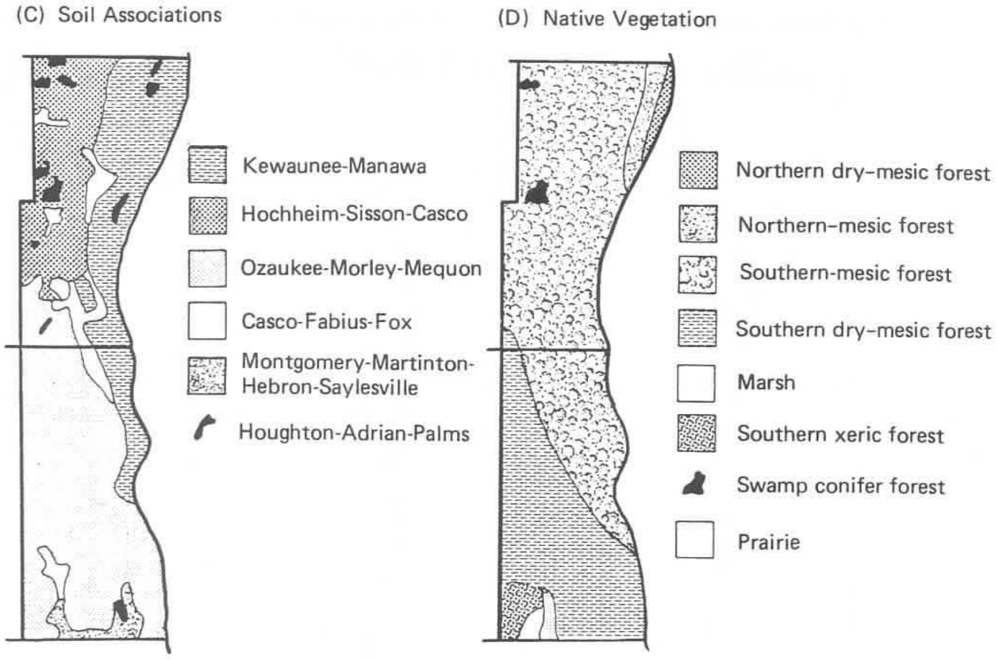


Fig. 3-3. Bedrock geology (A) and glacial geology (B) of the metropolitan Milwaukee region (redrawn from SEWRPC 1963), with maps of major soil associations (C) (redrawn from USDA-SCS 1970, 1971), and the native (presettlement) vegetation (D) (redrawn from Chamberlin 1973).

drained, silty soils typically found near waterways, foot slopes and depressions (USDA 1971). These soils are typical of most of Milwaukee County and southwestern Ozaukee County.

The Hochheim-Casco series (Typic Argiudoll and Typic Hapludalf) occur in western Ozaukee County. These well drained soils are formed in thin loess and loamy glacial material on ground moraines and outwash plains, and are characterized by moderate fertility and permeability (USDA 1970).

Vegetation

The pre- and postsettlement vegetation of metropolitan Milwaukee has been described by several authors (Chamberlin 1877, Shinners 1940, Whitford and Salamun 1954, Ward 1956, Curtis 1959). Three major vegetation types (prairie, northern forest, and the southern forest—after Curtis 1959) were originally present (Fig. 3-3).

The general vegetational pattern in the study area is oriented on a southwest-northeast axis. Prairie entered the extreme southwestern corner of Milwaukee County. Scattered oak openings were present in association with the prairie. These stands graded into the southern xeric (oak-hickory) forest. Southern dry-mesic (maple-red oak) forest covered most of Milwaukee County (Shinners 1940). The southern mesic (beech-maple) forest was discontinuous, primarily in the northeastern half of Milwaukee County and most of Ozaukee County. Patches of the southern xeric and southern lowland forest were found interspersed on xeric and depressional sites, respectively. Northern forest occurred in extreme eastern Ozaukee County and extended into northeastern Milwaukee County (Fig. 3-3). The northern mesic forest (northern hardwood or hemlock-hardwood forest), originally mapped as a narrow strip, entered Ozaukee County from the north, stretching southward along the lake shore to Port Washington (Chamberlin 1873). Patches of northern lowland, or swamp conifer forest (the wet phase of the northern forest) were also scattered throughout the study area (Hansen 1933).

Only a small portion of the two-county area was covered by prairie or northern forest. The greatest area was vegetated by southern forest. Three major upland southern forest communities were distinguished by Chamberlin (1877), Whitford (1951), and Curtis (1959) (Table 3-1). Chamberlin (1877) was probably the first to note that "no abrupt line of demarcation existed between" the communities.

At the moist end of the continuum, the southern lowland forest was once widespread throughout the study area. This type occurred along rivers and streamways, and in poorly drained upland depressions. There is little quantitative information describing the original lowland forest of this region, but it is probable that it was common before alteration of the water tables through deforestation and tiling of agricultural lands. The southern lowland forest has a great variety of tree species but exhibits widespread regional uniformity (Stearns 1965). Species composition normally includes silver maple (*Acer saccharinum*), black willow (*Salix nigra*), American elm (*Ulmus americana*), and swamp white oak (*Quercus bicolor*). Transition communities between the lowland and mesic forest were present in the upland depressions with green and black ash (*Fraxinus pennsylvanica* and *F. nigra*), red maple (*Acer rubrum*) and basswood (*Tilia americana*) gaining dominance (Ware 1955, Curtis 1959).

Table 3-1. Sources, Nomenclature, and Dominant Species in Various Treatments of the Upland Forests of Southern Wisconsin

Sources			
Chamberlin (1877)	Whitford (1951)	Curtis (1959)	Dominant tree species
Oak group	Oak-hickory	Southern xeric	*Quercus alba* *Q. velutina* *Q. macrocarpa* *Q. borealis*
Oak-maple group	Intermediate	Southern dry-mesic	*Quercus borealis* *Q. alba* *Tilia americana* *Acer saccharum*
Maple group	Maple-basswood	Southern mesic	*Acer saccharum* *Tilia americana* *Fagus grandifolia* *Ulmus rubra* *Quercus borealis* *Ostrya virginiana*

Land Use History

The present landscape pattern reflects its historical development. Before European settlement, the resident and transient Indian population had little impact. The Public Land Survey of exterior lines for the area (township and range) was completed by 1836 (SEWRPC 1970).

Early settlement was primarily by farmers. The process of clearing farms from the virgin forest was the "labor of a generation" (Schafer 1927). Settlers first came to the heavily forested region of Milwaukee and Ozaukee Counties in the early 1830s. The movement of settlers into the region was well under way by the spring of 1836. A territorial census taken in July 1836 assigned 2893 inhabitants to the original, much larger, Milwaukee County, which was established in 1834 (Schafer 1927).

The process of land selection by the settlers provides insight into land use patterning. During the great land sale of February and March 1839, nearly 500,000 acres were sold at $1.25 per acre. Since all the public lands were offered at a uniform price, the usual criteria for homestead selection included proximity to a spring or brook, proximity to a market, or to a market road, and/or proximity to the lake ports for sale of fuel wood and forest products. Another consideration was the general belief in the superiority of forested land over prairie land. The soils of the region were generally suitable except for some lowland areas and the narrow belt of heavy clay loam east of the Milwaukee River. In addition, it was a distinct advantage to have and maintain a woodlot for fuel and building materials. High, well-drained morainic ridges were used for roadways, a practice still evident in the region today. Homesteads were located near the ridges.

By 1860, over one-third of the land in Milwaukee County had been converted to plowfields, with another third also in farm ownership (Whitford and Whitford 1972). Wheat was the main cash crop from the time farming first started until about 1880.

The wheat monoculture soon depleted the upland soils, resulting in reduced yields and declining returns (USDA 1971). After the Civil War, the malting industry began to include barley and hops. After 1890, the popularity of these crops declined and gradually agriculture shifted to dairying, the major agricultural pursuit by 1920 (SEWRPC 1963). Grazing of woodlots was common.

The trends in farming were related to industrial and urban growth. The census of 1850 showed 31,077 persons in Milwaukee County. Between 1850 and 1860, the population more than doubled. Slow growth occurred between 1860-1870, but with increasing industrialization, a fivefold increase occurred between 1860 and 1900, doubling again between 1900 and 1930 (SEWRPC 1972). By 1970, Milwaukee County reported 1,054,249 residents.

For over 100 years, 1840 to 1950, urban growth and development occurred in a general outward expansion from the earlier established urban centers. But

> From 1950 to 1970 . . . a dramatic change occurred in this pattern of urban development in that large, scattered tracts of rural lands were subdivided for urban use, resulting in a highly dispersed, discontinuous, low-density development pattern, a pattern which has become known as "urban sprawl" (SEWRPC 1971).

The rapid population growth coupled with urban sprawl accounted for the conversion of more than 16,194 ha (40,000 a and 920 farms) of farmland to urban use in Milwaukee County between the late 1940s and 1959 (USDA 1971). In 1964, only 10,393 ha (25,670 a) of farmland remained in Milwaukee County, a decrease of 22% in five years (USBC 1964). The trend accelerated between 1964 and 1969 with only 7049 ha (17,412 a) remaining in farmland, a decrease of another 32%. The overall change during the decade, 1959 to 1969, was a 47% decrease in farm acreage and a 56% reduction in the number of farms (USBC 1969). Woodland, including woodland pasture, averaged only 8% of the county's farmland, and showed an overall decrease of 15% in area between 1964 and 1969.

In Ozaukee County, the total land in farms was 43,808 ha (108,205 a) in 1964. About 9% was wooded and 43% of the woodlands were actively grazed (USDA 1970). Ozaukee County experienced a 10% decrease in farmland between 1959 and 1969. The number of farms decreased by nearly 23% over the same period.

In Ozaukee County, the woodlands remaining for study were generally privately owned. In Milwaukee County, most were part of the Milwaukee County Park System (one of the finest in the country). The County Park Commission began an active program of land acquisition in 1910. Urban expansion in the county has eliminated many potential sites, and those remaining have accrued increased value for their open-space character in the heavily urbanized landscape (SEWRPC 1965).

Methods

Site Selection

In the metropolitan Milwaukee region, topography, soils, and climate are relatively uniform. Widely dispersed woodlots within an urban and agricultural matrix include southern mesic and southern dry-mesic forest types (Curtis 1959), dominant upland vegetation types now, as they were in presettlement time.

Forest island selection was based on several criteria. Each forest island ideally should:

1. be isolated from other islands, surrounded by a matrix of urban or agricultural land.
2. contain sugar maple in combinations representative of the southern mesic forest type (Curtis 1959).
3. be a remnant of original upland vegetation, not a newly established stand.
4. include all structural vegetation layers.
5. have no evidence of recent major disturbance.
6. have existed as a discrete unit long enough to have developed a mature forest edge.

Few stands fulfilled all of the criteria. Land use history of each stand was obtained by questioning owners, referring to earlier reports, and examining aerial photographs taken in 1937.

Forty-three woodlots of the southern upland mesic type were sampled in the metropolitan Milwaukee region between May and October, 1975 (Fig. 3-4). By design, islands were chosen to include a variety of sizes ranging from 0.03 to 40 ha.

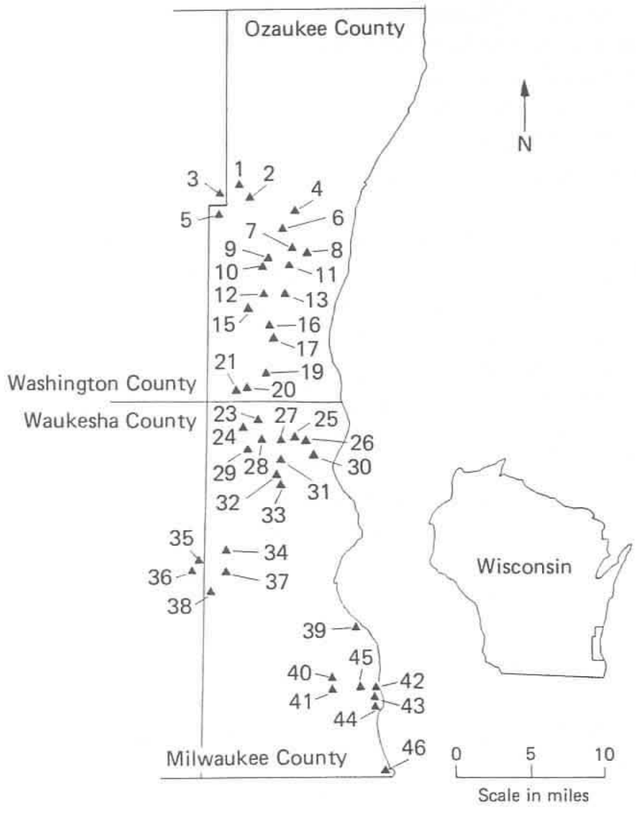


Fig. 3-4. Map showing the locations of the 43 forest islands studied in the metropolitan Milwaukee region.

Field Sampling Methods

Only the area bounded by the "edge trees" was sampled. Edge trees were defined as those trees exhibiting an asymmetrical bole, with a considerable clear-length on the interior side (forest-grown side) and heavy branching to the outside (open-grown side). These edge trees were not always present at the physical edge of the woodlot, but may have been some distance toward the island's interior. Woodlots adjacent to intensively managed land parcels develop mature edges and edge trees over time. If the adjacent land is later abandoned, or less intensively managed, succession occurs to the outside of the formerly stabilized edge (Wales 1972). However, the original forest area will remain delimited by its original edge trees. In some cases, the forest core was identical to current size and shape, but often the original core was considerably smaller and embedded in an expanding, second growth community. Vegetation outside of the edge trees was not sampled.

The vegetation of each island was sampled using the stratified-random line-strip method (modified from Lindsey 1955). Shrub, understory, and canopy strata were sampled contemporaneously using a series of nested rectangular plots (Fig. 3-5). In each stand, line-strips, separated by 25 m, were located systematically throughout the entire area. Species lists for each woodlot were compiled from the sample data plus extensive reconnaissance between plots and transects.

Canopy and understory strata were sampled in 10 × 25 m plots. All stems greater than 5 m tall and 2.5 cm diameter breast height (dbh) were recorded in three size categories: 2.5-5 cm (1-2 in.) dbh; 5-10.1 cm (2-4 in.) dhb; or, if over 10.2 cm (4 in.) dbh, by the exact diameter. Dead stems, recent windthrows, and stumps were also recorded. In most stands, 20 such plots were sampled, collectively totaling 0.5 ha. For stands $>$ 10 ha, a larger sample was obtained but line-strips were separated by a distance of 50 m. This modification insured representative coverage. Stands of 1 ha or less were full-tallied for canopy and understory strata.

The shrub layer was sampled in plots 2 × 12.5 m beginning at the midpoint of each 10 × 25 m plot. All woody species between 0.5 and 5 m tall were recorded. The num-

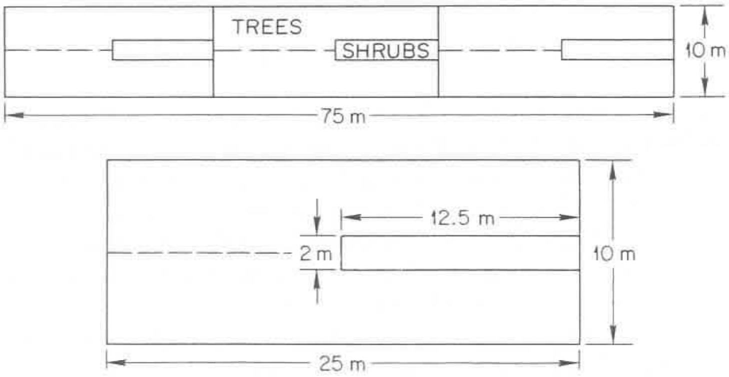


Fig. 3-5. Example of a line-strip, three plots in length, showing the arrangement of the nested plots. In the enlarged single plot (below), trees were sampled in the 10 × 25 m plot and shrubs in the 2 × 12.5 m plot.

ber of stems of each species present was recorded for each plot. Twenty plots were sampled in most stands, collectively comprising an area of 0.05 ha. In the smaller stands full-tallied for the canopy and understory, the shrub stratum was sampled using the line-strip technique, but with only 15 m separating the transects. Nomenclature follows Gleason (1952).

Data Analysis

Tables of species attributes were calculated for each structural stratum of each site (Levenson 1976). Species density was recorded as the number of stems per hectare. Frequency was defined as the percentage of plots in each stand in which the species occurred. Basal area (m^2/ha) was recorded for each species in each island. Relative density, relative frequency, and relative dominance were calculated and averaged to obtain the importance value expressed as a percentage for each species (Lindsey 1956). The importance value for species of the shrub stratum is the average of relative density and relative frequency only, since cover values were not measured.

Interisland comparisons were made using a hierarchical cluster analysis (Ward 1963, Veldman 1967). The technique produces clusters of mutually excluded stands, whose composition is more similar to others in the cluster than to stands in other clusters. The procedure reduces the number of clusters from n to $n-1$ to minimize information loss. Without modifying clusters already formed, the procedure was repeated until the number of clusters was systematically reduced from n to 1 (Ward 1963). With each grouping, an error index was provided, determined from the sum of within-group sums of squares. The analysis was based on the importance value of species present and on the "no value" information contributed by absent species.

Nonlinear regression analysis was performed to test the various models proposed by MacArthur and Wilson (1967), when examining the relationships between island size and degree of isolation with species richness. Likewise, the colonization and extinction models were nonlinear.

Results and Discussion

Overstory Structure and Composition

The forest woodlots ranged from dense, successional forests dominated by basswood (*Tilia americana*) with low basal areas to old-growth stands dominated by sugar maple (*Acer saccharum*) with a relatively high basal area. Stem density ($\geqslant 10.2$ cm) ranged from 240 to 929 stems/ha with an average of 442 (179 trees/acre). The average basal area (stems $\geqslant 10.2$ cm) for the 42 woodlots was 29.8 m^2/ha (130 $ft^2/acre$), but ranged from 21.5 to 43.3 m^2/ha (Table 3-2). This compares favorably with the 29.9 m^2/ha reported by Goff and Zedler (1968) for 125 xerophytic stands dominated by oaks (*Quercus* spp.) in southern-central Wisconsin. Such broad ranges of stem density and basal area are indicative of the structural variability found within the forest islands in metropolitan Milwaukee.

Of the 33 species in the canopy, nine species had a constancy value over 50% (Table 3-3). These nine species, in different proportions, dominated the 43 forest stands (Fig.

Table 3-2. Island Size and Woody Species Richness for Canopy and Shrub Strata of 43 Forested Islands in the Metropolitan Milwaukee Region, Wisconsin[a]

		Canopy stratum			Shrub stratum		Total no. of woody species
Site no.	Size (ha)	Total no. species	Density (no./ha)	Basal area (m^2/ha)	Total no. species	Density (no./ha)	
31	0.03	2	--	--	15	23,332	17
28	0.36	12	929	28.86	19	11,300	24
11	0.57	8	337	21.56	19	14,340	24
46	0.59	13	285	33.23	16	10,560	22
15	0.61	9	486	28.46	16	10,200	18
02	0.65	11	847	26.37	13	14,865	19
29	0.73	10	269	28.54	14	14,440	22
10	1.21	14	476	24.27	24	15,223	31
32	1.40	16	331	22.78	20	13,872	27
13	1.50	9	448	30.52	24	9,480	28
08	1.54	11	445	32.36	13	13,700	19
20	1.58	10	494	22.81	25	20,075	27
09	1.62	11	265	21.51	17	18,720	24
26	1.70	8	465	30.63	22	30,050	24
12	1.98	13	360	28.30	17	8,984	27
05	2.06	10	495	31.25	24	16,700	28
21	2.19	17	542	29.62	35	14,060	42
03	2.23	9	516	32.76	22	10,900	25
23	2.35	11	447	31.00	24	14,175	27
35	2.39	14	540	37.44	27	12,820	35
24	2.43	12	446	29.99	22	29,900	27
07	2.43	18	576	33.65	16	21,900	31
25	2.47	15	506	29.49	25	18,200	33
27	2.51	16	684	29.52	23	23,360	32
43	2.83	10	326	33.79	14	13,420	20
19	2.91	14	478	30.13	23	15,600	31
33	3.12	17	358	25.68	26	28,540	34
42	3.24	13	304	28.42	13	6,260	25
44	3.97	15	436	43.30	8	21,080	21
30	4.09	13	366	33.49	18	23,520	28
41	4.13	12	358	32.03	11	10,058	20
17	4.25	8	464	31.10	21	18,960	23
37	4.49	11	330	31.44	20	18,800	28
34	5.47	11	240	22.49	19	23,360	28
06	6.48	7	356	27.22	18	16,180	19
16	7.21	12	550	32.00	13	21,420	20
40	7.81	11	416	36.12	20	16,040	24
45	7.93	12	276	31.04	17	12,050	21
39	11.46	15	474	33.02	16	14,380	24
04	14.53	7	398	31.94	19	12,317	21
38	18.34	11	366	31.07	16	12,200	25
36	21.05	12	348	29.80	26	21,100	27
01	39.96	13	524	24.30	18	18,057	21
	Mean	12	442	29.84	19	16,616	25
	SD	± 3	±141	± 4.36	± 5	± 5,641	± 5

[a] Canopy stratum includes all species more than 5 m tall and 2.5 cm dbh, but density and basal area were calculated only for stems greater than 10 cm dbh. The shrub stratum includes all woody species from 0.5 to 5 m tall.

Table 3-3. Summary Values for All Canopy Species (Ranked by Importance Values), Occurring in 43 Forest Islands in Southeastern Wisconsin[a]

Species	Constancy (%)	Density (no./ha)	Basal area (m^2/ha)	Mean importance value
Acer saccharum Marsh.	100.0	118	7.76	26.24
Fagus grandifolia Ehrh.	76.7	98	5.76	15.32
Tilia americana L.	88.4	81	4.84	14.59
Quercus borealis Michx.	83.7	35	5.92	10.16
Fraxinus americana L.	95.3	38	2.95	9.34
Quercus alba L.	60.5	27	3.33	5.56
Ostrya virginiana (Mill.) K. Koch	88.4	33	0.55	5.21
Prunus serotina Ehrh.	79.1	28	0.84	3.83
Ulmus rubra Muhl.	72.1	15	0.76	2.78
Acer rubrum L.	37.2	17	1.23	1.41
Carya cordiformis (Wang.) K. Koch	44.2	6	0.22	0.70
Crataegus succulenta Link.	30.2	10	0.15	0.66
Juglans cinerea L.	30.2	4	0.49	0.53
Carya ovata (Mill.) K. Koch	14.0	10	0.54	0.48
Betula papyrifera March.	18.6	10	0.62	0.43
Ulmus americana L.	41.9	4	0.13	0.39
Fraxinus pennsylvanica March.	23.3	8	0.37	0.38
Acer saccharinum L.	4.7	36	3.72	0.35
Quercus macrocarpa Michx.	9.3	6	1.32	0.33
Juglans nigra L.	7.0	11	1.87	0.26
Fraxinus nigra Marsh.	11.6	9	0.20	0.21
Populus grandidentata Michx.	2.3	47	1.61	0.13
Quercus bicolor Willd.	9.3	4	0.35	0.11
Amelanchier laevis Wieg.	11.6	3	0.05	0.10
Populus tremuloides Michx.	9.3	4	0.14	0.10
Catalpa speciosa Warder.	2.3	12	0.80	0.08
Acer negundo L.	4.7	6	0.11	0.07
Carpinus caroliniana Walt.	9.3	3	0.04	0.06
Betula lutea Michx.	4.7	3	0.28	0.04
Celtis occidentalis L.	2.3	4	0.50	0.03
Pyrus malus L.	4.7	3	0.05	0.03
Crataegus punctata Jacq.	2.3	2	0.03	0.02
Cornus alternifolia L.	2.3	1	0.02	0.02
Totals		442	29.84	99.95

[a] Values for the mean density and mean basal area are based on only the stands in which the species was present. Mean Importance Value is the average of the sum of the relative values of frequency, density, and dominance (maximum = 100).

3-6). Forty of the habitat islands were dominated by nearly every possible combination of only six species: sugar maple, American beech, white ash, basswood, red oak, and white oak. The final three clusters of the dendrogram (Fig. 3-6) were sufficiently different to be recognized as major groups: Maple and Beech Group, Maple Group, and Basswood Group. The separation of the Maple Group from the Maple and Beech Group

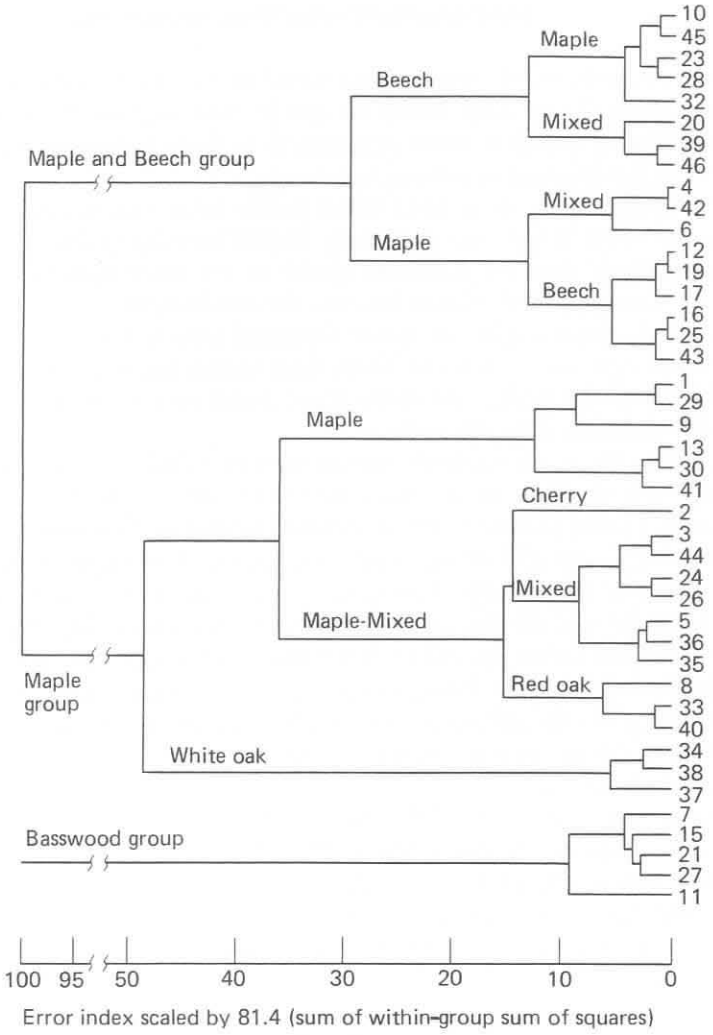


Fig. 3-6. Dendrogram of the results of the cluster analysis of the canopy stratum data for 42 forest islands based on species composition and importance values. Site 31 was excluded from the analysis because of insufficient sample size (see Table 3-2). The leading dominant(s) of each major group is listed.

was the result of the dominant role played by beech. Interestingly, this separation is the same as that recognized by Chamberlin (1877) over a century ago. The Basswood Group was sufficiently different in composition and structure to remain separated from the other groups. The five stands in this group appeared to be successional in nature. Three were solely dominated by basswood (Sites 7, 11, and 15). In the other two, basswood, red oak and white ash shared dominance.

Shrub Stratum Composition and Structure

Sixty-six different woody species were found in the shrub stratum of the 43 forest habitat islands (Table 3-4). Thirty-six species were considered true shrubs, species whose maximum potential height restricted them to the subcanopy. The remaining 30 species had the potential of entering the canopy.

Stem density in the shrub layer varied greatly from stand to stand. Stem densities for the 43 forest islands averaged nearly 16,700 stems/ha (Table 3-2). Choke cherry and sugar maple were the dominant species of the shrub layer (Table 3-4). Choke cherry was sampled in all islands, and was the dominant or codominant shrub in 95% of the stands. Sugar maple, the second dominant species, followed by white ash were each absent from only one stand. These three species accounted for 67% of all stems recorded. Dogberry (*Ribes cynosbati*) shared dominance in 24% of the stands and the hybrid honeysuckle (*Lonicera bella*) in 14%.

Only nine species in the shrub stratum were classified as exotics, i.e., not native to eastern North America. Of the nine, only three occurred in more than two islands. Nightshade (*Solanum dulcamara*) and common buckthorn (*Rhamnus catharticus*) were present in 42% and 30% of the stands, respectively. Bird dispersal was suggested for both species as they produce multiseeded berries and drupes. Both species appeared most successful in disturbed sites with wet-mesic conditions. Only the hybrid honeysuckle (*Lonicera bella*) was widely distributed, occurring in 58% of the stands, often with locally high densities. Honeysuckle is an opportunistic species, entering the forest in an opening or edge, prospering, and finally declining as the canopy closes. None of the exotic shrub species appeared able to survive under the closed forest canopy of the southern mesic forest.

In general, the shrub flora of the islands reflected the disturbance history with varying degrees of species richness attributable to the balance of elements of both the pioneer and terminal communities, as well as exotics. Stands with a high species richness in the shrub layer were characterized either by mixed communities without dominants or by only weakly dominant species, i.e., low relative densities of choke cherry and/or sugar maple.

Species-Area Relationship

The species-area relationship of Arrhenius (1921), Preston (1960) and MacArthur and Wilson (1967) is depicted for all woody species greater than 0.5 m tall (Fig. 3-7). The function

$$S = kA^z$$

where S is the number of species in an area A, and k and z are constants, was fitted to the points. The best fit was the near-linear function approximating the average number of species for the 43 islands but relatively independent of island size, indicating little correlation between island size and species richness ($R^2 = 0.01$). It is evident that, as attractive as the ability to predict plant species richness by island size appears, additional variables must be considered. Although many researchers have shown an

Table 3-4. Summary Values for All Species Occurring in the Shrub Stratum of 43 Forest Islands in Southeastern Wisconsin[a]

Species	Constancy (%)	Density (no./ha)	Importance value
Prunus virginiana L.	100.0	6863	30.28
Acer saccharum Marsh.	97.7	3012	16.64
Fraxinus americana L.	97.7	1391	10.18
Prunus serotina Ehrh.	90.7	615	6.35
Ribes cynosbati L.	74.4	1026	4.67
Lonicera bella Zabel.[b]	58.1	1273	4.19
Fagus grandifolia Ehrh.	69.8	472	3.47
Tilia americana L.	81.4	431	3.18
Ribes americanum Mill.	72.1	601	2.82
Ostrya virginiana (Mill.) K. Koch	65.1	197	1.51
Vitis riparia Michx.	58.1	214	1.42
Carya cordiformis (Wang.) K. Koch	62.8	127	1.30
Cornus stolonifera Michx.	25.6	1513	1.27
Viburnum lentago L.	53.5	315	1.22
Ulmus rubra Muhl.	58.1	138	1.04
Cornus racemosa Lam.	37.2	384	0.99
Populus grandidentata Michx.	2.3	300	0.99
Hamamelis virginiana L.	25.6	399	0.76
Rubus occidentalis L.	44.2	173	0.76
Viburnum opulus L.	20.9	708	0.72
Solanum dulcamara L.[b]	41.9	244	0.70
Zanthoxylum americanum Mill.	41.9	115	0.70
Viburnum acerifolium L.	23.3	406	0.62
Crataegus succulenta Link.	32.6	106	0.48
Viburnum rafinesquianum Schult.	20.9	347	0.47
Cornus alternifolia L. f.	25.6	177	0.45
Menispermum canadense L.	25.6	359	0.42
Dirca palustris L.	23.3	136	0.42
Sambucus canadensis L.	20.9	76	0.42
Fraxinus pennsylvanica Marsh.	9.3	167	0.34
Quercus borealis Michx. f.	32.6	70	0.34
Rhamnus catharticus L.[b]	30.2	69	0.34
Crataegus punctata Jacq.	32.6	45	0.29
Acer negundo L.	20.9	61	0.22
Carpinus caroliniana Walt.	18.6	35	0.17
Lonicera prolifera (Kirchner) Rehder	14.0	132	0.16
Amelanchier sp. L.	16.3	55	0.14
Acer rubrum L.	18.6	38	0.14
Sambucus pubens Michx.	7.0	247	0.12
Parthenocissus quinquefolia (L.) Planch.	14.0	55	0.12
Viburnum lantana L.[b]	4.7	163	0.11
Fraxinus nigra Marsh.	7.0	87	0.11
Euonymus atropurpureus Jacq.	4.7	293	0.10
Rhamnus frangula L.[b]	4.7	173	0.08
Ulmus americana L.	11.6	25	0.07
Quercus macrocarpa Michx.	4.7	80	0.06
Smilax hispida Muhl.	2.3	280	0.05
Carya ovata (Mill.) K. Koch	4.7	95	0.05
Juglans nigra L.	4.7	30	0.04
Betula papyrifera Marsh.	2.3	100	0.03

Table 3-4 (continued)

Species	Constancy (%)	Density (no./ha)	Importance value
Acer saccharinum L.	2.3	120	0.03
Juglans cinerea L.	2.3	63	0.03
Forsythia suspensa (Thunb.) Vahl.[b]	2.3	120	0.02
Ptelea trifoliata L.	2.3	40	0.02
Celtis occidentalis L.	4.7	44	0.02
Rosa sp. L.	2.3	100	0.02
Rhus radicans L.	4.7	20	0.02
Berberis thunbergii D. C.[b]	2.3	150	0.02
Euonymus alatus (Thunb.) Sieb.[b]	2.3	20	0.01
Populus tremuloides Michx.	2.3	20	0.01
Quercus alba L.	2.3	20	0.01
Thuja occidentalis L.	2.3	25	0.01
Rhus typhina L.	2.3	15	0.01
Celastrus scandens L.	2.3	72	0.01
Rubus hispidus L.	2.3	15	0.01
Acer ginnala Maxim.b	2.3	40	0.01
Totals		16,627	100.00

[a] Mean density is based on stands in which the species was present. Importance Value is the average of the sum of the relative values of density and frequency (maximum = 100).

[b] Introduced exotics.

increasing number of species with increasing island size, another major consideration is the environmental heterogeneity of the community. Niering's (1963) floral study of Kapingamarangi Atoll indicated that increasing the areas of sand did not add to the floral richness. The flora remained restricted to the few species adapted to the xeric habitat. An increase in area added more of the same habitat, but no additional new habitats. However, the establishment of a freshwater lens in islets of 1.4 ha and larger (Wiens 1962) created increased habitat variety which supported more species. Johnson et al. (1968) found island area to be the best single predictor of plant species diversity, but concluded that environmental richness was also significant. Qualitatively different environments result from increasing topographic, edaphic, and/or climatic diversity (Heatwole and Levins 1973).

The woody species composition of forest woodlots in southeastern Wisconsin was restricted by similar factors (Levenson 1980). An increase in area very often added more of the same habitat. It was not until variations in soil, relief, or disturbance were present that changes in species variety were realized. The southern mesic forest community of southeastern Wisconsin is composed of a relatively few, shade tolerant woody species adapted to the mesic forest's interior: sugar maple, beech, ironwood, and slippery elm (Curtis 1959). Vegetative reproduction in the form of root and stump sprouts increases the chances for these species to persist and compete under the full canopy. Additional species present in the forest islands such as white ash, red oak and black cherry are less shade tolerant. Their presence is often the result of disturbance and redevelopment through gap-phase reproduction (Watt 1947, Bray 1956).

Disturbance, whether natural or man-induced, is a major variable controlling woody species richness in forest woodlots. In the southern mesic forest ". . . it is clear

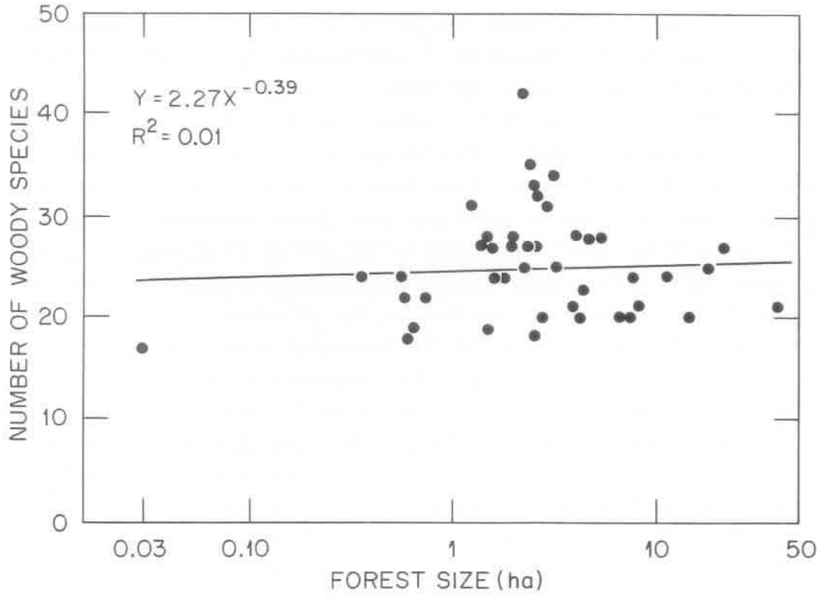


Fig. 3-7. Total number of woody species as a function of island size ($S = kA^z$).

that the degree of success of the intolerant trees and hence the degree of species mixture to be found in the forest is proportional to the chances for disturbance" (Curtis 1959). In the agro-urban matrix of metropolitan Milwaukee, the forest islands owe their existence, isolation and composition primarily to man-induced disturbances. In northwestern Ohio, Tramer and Suhrweir (1975) concluded that human interference was a major variable in affecting species richness of the elm-ash-maple woodlots. Slack et al. (1975) also indicated that increased disturbance contributed to an increased number of exotic species as well as to an increased overall diversity of vascular plants and bryophytes on 54 islands in Lake George. Islands of the Puerto Rican Bank have also received heavy human disturbance by littering, cutting of trees and shrubs, making of paths, and abandonment of unwanted pets which leads both to local extinctions and to establishment of previously absent species (Levins and Heatwole 1973). Many of the consequences of human usage of the islands in Ohio, New York, and Puerto Rico are similar to those in metropolitan Milwaukee. Auclair and Cottam (1971) indicated that, coupled with forest island isolation, heavy usage was the most critical aspect of woodlot ecology.

Frequent disturbance results in a shift toward a more xeric habitat with greater light, greater transpiration stress, and more variable temperature and moisture levels. Disturbance destroys the mesic "stabilizing mechanisms" to favor species with pioneer tendencies, in contrast to more mesic species (Curtis 1956, Auclair and Cottam 1971).

Disturbance in the isolated forest woodlots can be quantified indirectly by a number of variables. Stem densities, percentage canopy cover and size-class distributions are all variables traditionally used to determine the amount of disturbance a woodlot has undergone. In the southern mesic forest, canopy closures may be one of the major variables. Gaps in the canopy reduce the mesic character of the forest interior. In the old-growth, southern mesic forest, the gaps in the canopy are a result of the number of dead standing, cut or fallen stems. Following this logic, Table 3-5 presents a list of possible indicators of disturbance and values for each site.

Using a stepwise multiple linear regression program, three of these variables were found to be significant in determining the species richness, a function of the basal area of sugar maple, the proportion of dead stems and the amount of dead basal area in the stand. More mature stands in this region have greater dominance by sugar maple, so that species richness should be inverse to the density of large stems of sugar maple. Sugar maple forms a very dense canopy and is largely responsible for maintaining the mesic conditions of the forest interior. On the other hand, dead stems may indicate that the canopy has been opened and that intolerant, or successional, species were able to invade the resultant gap. Therefore, the proportion of dead stems is an indicator of the potential number of disturbance sites within the stand. In the mature forest, the size of the stems is also important. That is, the larger the dead trees, the larger will be the gap in the canopy, to a point. Trees of small diameter may not reach the canopy and may be understory components. However, a spurious correlation exists between the proportion of dead stems and their basal area (Table 3-6). Excluding the dead basal area, the remaining variables account for approximately 21% of the variance of species richness of the forested woodlot islands. The following equation is statistically significant at the $P < 0.01$ level:

$$\text{Species richness} = 24.8 - 0.2X_1 + 0.3X_2$$

where X_1, basal area of sugar maple/ha; X_2, proportion of dead stems.

The variables of woodlot size and disturbance level are not necessarily mutually exclusive and may be analogous for woodlots less than some threshold size. As islands become smaller, younger, or more disturbed, the entire island may become functionally edge. Figure 3-8 depicts several hypothetical woodlots of varying sizes, each surrounded by an edge, X units wide. The depth of the edge has been assumed to remain constant. As woodlot area decreases, edge and interior areas also decrease; but the edge/interior ratio increases. At some point, designated (a), the woodlot has become sufficiently small that the edges from all aspects merge at the woodlot's center. Woodlots of sizes smaller than (a) are not capable of maintaining mesic conditions and have become, functionally, entirely edge. Woodlot size (a) is theoretically the minimum size at which

Table 3-5. Potential Indicators of Disturbance in Southern Wisconsin Forest Islands

Number	Characteristic
1.	Human population density per census tract
2.	Living basal area per hectare
3.	Dead basal area per hectare
4.	Living stem density per hectare
5.	Dead stem density per hectare
6.	Sugar maple density per hectare
7.	Sugar maple basal area per hectare
8.	Sugar maple importance value
9.	Proportion of dead basal area [i.e., 3 ÷ (2+3)]
10.	Proportion of dead stems [i.e., 5 ÷ (4+5)]

Table 3-6. Matrix of Correlation Coefficients of Species Richness and Each Index of Disturbance (Table 3-5)

	Species richness	Forest island size	Log_{10} human population	Living basal area	Dead basal area	Live stem density	Dead stem density	Sugar maple stem density	Sugar maple basal area	Sugar maple importance value	Proportion dead basal area
Forest island size	-0.08										
Log_{10} human population	0.12	-0.03									
Living basal area	-0.26	0.04	0.08								
Dead basal area	-0.10	-0.13	-0.40	-0.33							
Live stem density	0.17	-0.20	-0.33	-0.06	0.40						
Dead stem density	0.31	-0.21	-0.33	-0.30	0.60	0.66					
Sugar maple stem density	-0.23	-0.10	-0.30	0.34	0.10	0.05	-0.19				
Sugar maple basal area	-0.38	0.01	-0.04	0.54	-0.07	-0.30	-0.38	0.65			
Sugar maple importance value	-0.35	-0.00	-0.14	0.34	0.04	-0.31	-0.38	0.83	0.90		
Proportion dead basal area	-0.04	-0.18	-0.37	-0.44	0.97	0.33	0.59	0.04	-0.10	0.04	
Proportion dead stem density	0.38	-0.11	-0.22	-0.43	0.44	0.29	0.88	-0.28	-0.36	-0.34	0.48

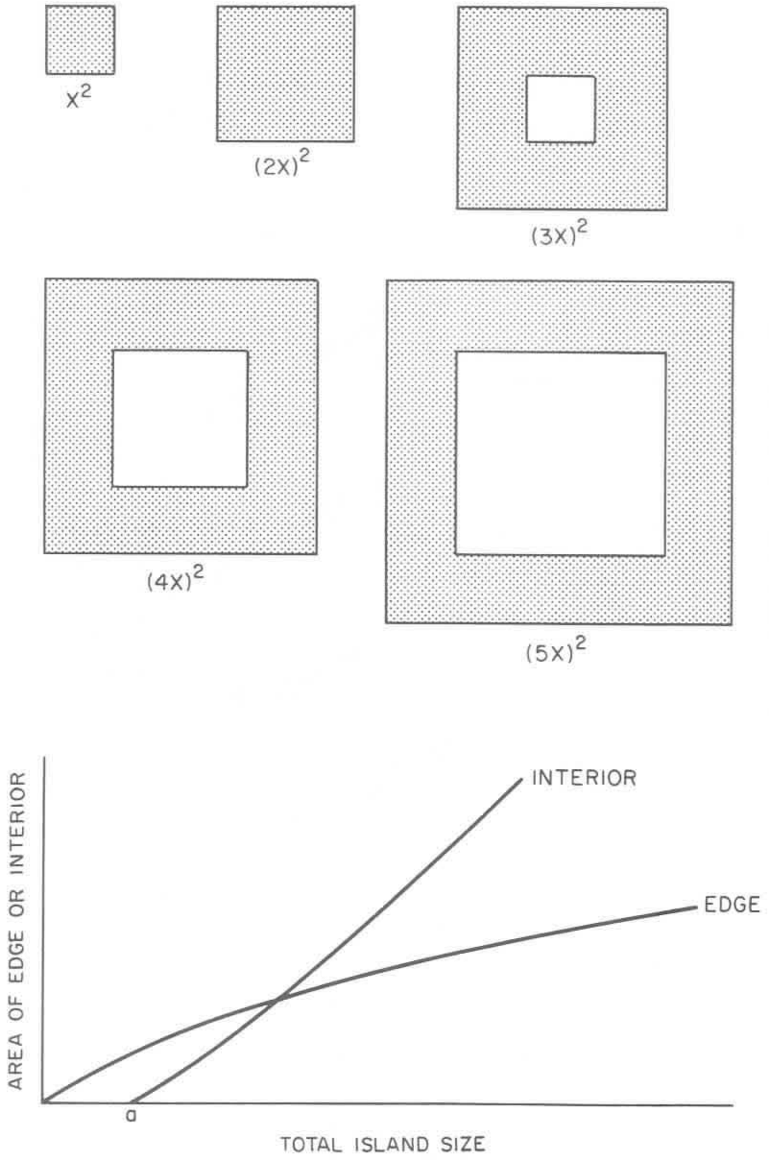


Fig. 3-8. Hypothetical forest islands with varying perimeter lengths. The depth of the edge community (stippled) has been held constant at X units. The area of edge increases with an increase in island size. At point "a" (lower graph), interior conditions begin to form. The area of interior increases at a steeper rate than the area of edge for nearly square or circular islands.

"interior" can be differentiated from "edge" and where mesophytic conditions might exist. The relationship between the area of edge, area of interior, and total area can be further demonstrated for forest remnants of a generally round or square shape (Fig. 3-8). Actual slopes of the edge and interior functions could be determined from field analysis.

These assumptions were related to the species richness and community dynamics of the mesic forest woodlots of metropolitan Milwaukee (Levenson 1976). When the interior is of sufficient size to maintain the low light, mesophytic conditions, sugar maple, and beech (if present) are favored over the less tolerant species. With smaller interior areas, the mesic species are "rejected" in deference to those species which possess pioneer tendencies. The relationship between the area of edge (or disturbance) and the potential number of woody species can be demonstrated graphically (Fig. 3-9). Given enough area and variation in conditions, the number of woody species which could exist in an edge environment increases to become asymptotic to the number of woody species of the region, i.e., in southeastern Wisconsin. The function increases rapidly since the major constraint is adequate physical space to accommodate an individual of a new species. The locally high stem densities generate a steep curve of the general form of the species-area function. With the formation of interior conditions, theoretically at size (a), the relationship of woody species in the interior of a woodlot, as approximated by the area bounded by edge trees, follows the general form of a depletion curve with increasing island size (Fig. 3-9). The curve approaches the number of shade-tolerant, mesic species of the region. A general expression describing the woody species richness for the interior of southern mesic forest woodlots can be derived by combining the two previous functions (Fig. 3-9). The resultant function illustrates how species richness responds to the transition of woodlot character from one of all edge to one of largely mature forest. Oscillations occur in the number of species present in the mesophytic environment, whose amplitude and frequency are a function of the intensity and duration of perturbations.

Fitting the theoretical curve to sample data, total woody species richness of the sampled core increased with woodlot size to approximately 2.3 ha. Beyond this size, species richness declined. Levenson (1976) interpreted this as the theoretical point (a)—the minimum size at which the edge community could be differentiated from the interior community. This interpretation compares reasonably with the 2 ha island size at which tree species richness stabilized in the mature oak forests of New Jersey (Forman and Elfstrom 1975). Earlier, Vestal and Heermans (1945) established a similar value (1.6 ha) for "minimum stand" size (the minimum reference area to identify a stand as a particular association or variant) in central Illinois.

The species depletion curve leveled off near an island size of approximately 3.8 ha (9.4 acres), designated as point (b). Point (b) is significant as it probably represents the smallest size at which a mature, southern mesic forest can perpetuate its interior conditions while sustaining limited, random perturbations (Loucks 1970).

The species composition and structure of the remnant forests is more readily understood when examined in light of relatively recent historical events and land use patterns throughout the region. The reduction of the regional forest complex over the past century did not preserve the full variety of environments and associated species of the original forest. Most fertile upland sites were converted to agriculture (Curtis 1959) while the land remaining in forest was generally wet, stony, or rough and otherwise undesirable for agriculture. Thus, by the time urbanization was underway, the choicest upland forest sites had already disappeared. Similarly, Auclair and Cottam (1971) indicated that the majority of the remnant forests in south-central Wisconsin were located on steep slopes of low agricultural value. This study was restricted to upland sites, but the numerous lowland species present in the stands suggest that many

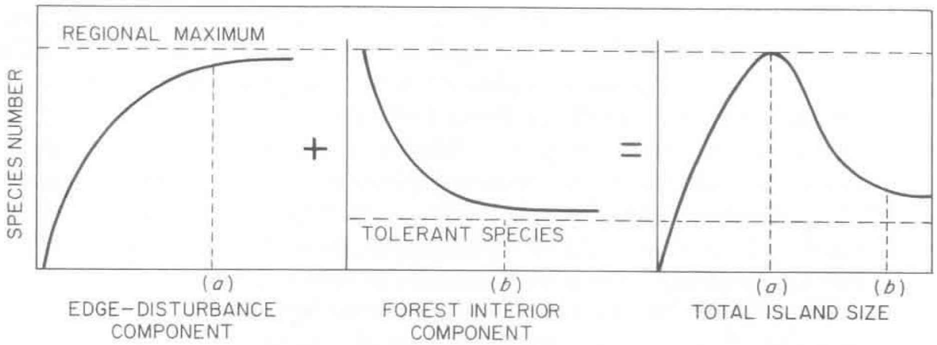


Fig. 3-9. The relationship between the amount of edge and potential woody species richness. Left: Given enough area and variety of conditions, the number of species that could exist becomes asymptotic to the number of woody species of the region. At some point (a), interior conditions begin to form. Center: Response of woody species to an interior environment characterized by low light levels and mesic conditions. The depletion curve levels off at the number of tolerant, mesophytic species in the region, point (b). Right: Curve combining the exponential and depletion functions that simulates the field data from southeastern Wisconsin forest islands.

of these remaining upland sites are actually imperfectly drained upland depressions. The presence of the somewhat poorly drained Mequon silt loam soil further supports this position (Levenson 1976).

Initial isolation and disturbance of the remnant stands occurred between 1850 and 1940. All woodlots of the region were probably selectively logged during the last century and some were clear-cut, while grazing of the woodlots in southern Wisconsin was a widespread practice (Auclair and Cottam 1971, Whitford and Whitford 1972). Owners and neighbors of isolated forests indicated that nearly all woodlots studied were grazed 40-50 years ago (1930-1940). Grazing was a constituent of a major regional ecosystem disturbance during the drought and depression years of the mid-1930s when forage crops were in limited supply and the woodlots were a source of inexpensive, emergency forage. Coupled with the drought, the impact of the grazing and soil compaction by the large livestock population was devastating. Although grazing was largely terminated by the 1950s, the forest structure today is, in large part, a result of natural recovery following that period.

The species turnover in mesic forest communities was viewed by Loucks (1970) as "repeating waveform phenomena triggered by random perturbations" at intervals of 20-200+ years. He suggested that peak species diversity in the mesic forest was achieved 100-200 years after secondary succession had been initiated, a period when members of both the pioneer and stable communities were present. As intolerant species drop from the community with time, species diversity declines. The self-perpetuating forests thus are less diverse than the later successional stages leading to them.

Species diversity of the canopy and understory strata of the 43 habitat islands appears to conform to the model described by Loucks (1970), but at a local, not a regional scale. His random perturbations were large or widespread, and in the framework of a regional forest. Perturbations in the isolated islands may be much smaller in magnitude, i.e., windthrow, death by old age, vandalism, etc., but occur more frequently, maintaining the stand in a subclimax condition. Instead of destruction of all species triggering widespread secondary succession as in Louck's (1970) model, the woodlots suffer chiefly localized disturbance with patches of successional species intermixed among the older, large climax species. More disturbance patches result in a higher species richness for the island. Suhrweir (1976) also interpreted this phenomenon as maintaining species richness near the peak of the waveform. Frequent disturbances coupled with isolation prevent some habitat islands from reaching the expected structure and composition of the terminal stages and result in the moderately high species richness.

Isolated forest woodlots are completely surrounded by a protective edge when the concept is expanded to include the canopy—the upper edge. When a large tree dies, or is windthrown, forest structure and composition are likely to change rapidly. Gaps within the forest function in much the same manner as the edge. The frequency of gaps can contribute greatly to making a large woodlot in reality no more than a highly convoluted edge.

Similarly, removing an edge or dividing a large woodlot with an access road or transmission line also may destroy the mesophytic environment of the system. A large woodlot is more capable of sustaining localized perturbations. However, as woodlot size declines, a perturbation in the edge-canopy becomes more catastrophic. A small woodlot (< 2.3 ha) dominated by sugar maple probably could not persist longer than the remaining canopy trees themselves. Conditions within a small woodlot, with its protective edges removed, shift to favor intolerant species and to reject the "more conservative mesic types" (Auclair and Cottam 1971). Recently isolated segments most commonly shift from a mesophytic to a more xerophytic community which is in dynamic equilibrium with the surrounding environment. Over time, with the formation of a complete canopy and dense edges, the woodlot may again provide conditions favorable to the development of a mesophytic community, if it is of sufficient size.

The inverse relationship between relative density and success of sugar maple and white ash seedlings in the urban and disturbed rural habitat islands is a manifestation of the dynamics. Sugar maple seedling densities were lower in the urban and disturbed sites while white ash appeared to reach somewhat higher densities (Levenson 1980). The situation was reversed in the less disturbed rural islands, even though sugar maple and white ash occupied similar positions in the canopy. The reduced success of sugar maple in the metropolitan woodlots had been observed earlier and was partially attributed to heavy rabbit browsing—an impact of reduced woodlot size and increased edge habitat. There was also some indication that suitable seedbeds for sugar maple were absent in the more xeric and compacted soils of the urban sites. Greller (1975) reported a general scarcity of seedlings of canopy species in the municipal forests of Queens County, New York, both in high disturbance areas as well as in the less-disturbed portions of the park. These problems require further investigation as they have a direct bearing on the successional dynamics and future composition of urban and other isolated forests.

The loss of American and slippery elm due to Dutch-elm disease is another perturbation that has created conditions favorable for white ash. The relative contribution of white ash in the upland forests of the Milwaukee region has increased in recent years.

Whitford and Salamun (1954) reported an average importance value for white ash of 4.3% compared to 9.3% in this study. The number of stands in which white ash was present are comparable (95% in each study), but the relative contribution to the importance value has more than doubled. In sites common to both studies (Sites 30, 33, 37, 38 and 40), an increase of white ash is evident while the elms showed a marked decline. Most of the other species have retained similar importance values over the past 24 years. Relatively high abundance of white ash in the smaller size classes accounts for its increased importance values (Levenson 1980). White ash reached a high average importance value in the shrub stratum just as it had in the canopy, averaging almost 1400 stems/ha (Table 3-4).

The replacement of elm by white ash is logical as the genera have similar ecological requirements. White ash has become a major component of the second growth forests of southeastern Wisconsin. Less frequent in old-growth forests, its presence is attributed to the ability to persist in dense shade until a canopy opening occurs (Cope 1948, Fowells 1965). White ash is shade tolerant when young, capable of surviving with little growth under a full canopy at less than 3% full sunlight (Cope 1948), but becomes less tolerant with increasing age. Canopy openings formed by the death of elms, or other disturbance, create areas of localized secondary succession within the stand. When exposed to full light, ash seedlings are capable of rapid growth (Guenther 1951).

The role of white ash in the mesic forest is similar to that described for black cherry (*Prunus serotina*) in the xeric forests of south-central Wisconsin (Auclair and Cottam 1971). The relative importance value of black cherry was reported to average over 50% in the sapling and small tree sizes, and in some stands it was the only species in those strata. To a lesser extent, I recorded relatively high densities of black cherry in the smaller size classes only in the dry-mesic sites dominated by white oak and characterized by less dense canopies (Levenson 1980). White ash is more successful in the southern mesic forest, although both species act as opportunists responding to disturbances in the canopy, as suggested by higher stem densities in the shrub layer (Table 3-4).

For the community to approach a terminal equilibrium, a source of propagules for each potential component of the community must be close enough to insure the arrival of viable seeds in the stand. Once a species is eliminated from a woodlot, it may not be possible for it to reestablish. Auclair and Cottam (1971) report that species which are bird-dispersed (*Prunus* spp. and *Celtis* spp.) have a considerable advantage over the heavy-seeded mammal-dispersed or wind-dispersed species (*Quercus* spp., *Carya* spp., *Acer* spp.). They further report that the isolation of woodlots in south-central Wisconsin has localized the distribution of sugar maple and is the major obstacle to the further successional development of the oak forests (*Quercus* spp.) to sugar maple-basswood, the terminal forest for the region. American beech, another climax species in the forests of southeastern Wisconsin, offers a similar example. As beech is unable to produce a viable mast in this region (Ward 1956), its reproductive potential is limited to root sprouts. Thus, the elimination of beech from an existing island greatly diminishes the probability of natural reestablishment.

The majority of isolated forest habitat islands in metropolitan Milwaukee are bounded by agricultural, urban, or other intensive land uses. The retention of extensive tracts of original forest was proposed by Gomez-Pompa et al. (1972) as the only way to reconstruct tropical rain forests which are unable to develop toward maturity when the tracts are widely separated by agricultural land. Considerable distances exist between the few large islands remaining in the agro-urban landscape (Levenson 1976, Davis and Glick 1978). Various authors have suggested that islands be connected by strips of protected habitat, or green belts. However, land availability and cost almost prohibit such acquisition in the metropolitan matrix. In the rural sectors, fencerows, windbreaks, utility and transportation rights-of-way often provide a source of seeds, cover, breeding grounds, and avenues for seed dispersal. These habitat corridors contribute greatly to the overall texture of the landscape. However, most of the woody species of the fencerow corridors are the same as those of the forest edge, not its interior. Fencerows are not unlike edge communities in terms of stem and foliage density, and are often extensions of the forest edge community with the same wildlife-initiated origins. They are of particular value when they link otherwise isolated woodlots.

Aerial reconnaissance of the Milwaukee metropolitan area indicated an extensive interstitial forest (Detwyler 1972) composed of rapidly growing, traditional lowland species, e.g., American elm, silver maple, and various ashes. In recent years, rapid development and urban sprawl compounded by heavy elm mortality have left large areas devoid of interstitial forest cover. These circumstances provide an unusual opportunity to restore a portion of regional ecosystem variety. Encouragement of the use of ecotypically local, upland trees as street and yard plantings could provide seed sources, increase species richness, and overcome the problems associated with interisland distance. Landscaping with native shrubs and ground cover in residential and commercial areas could supplement the lesser forest strata while providing widespread habitat and food sources for birds and small mammals.

In addition to removing associated migration and fencerow corridors, urban systems tend to select for smaller woodlot island sizes. These changes in landscape structure can have serious consequences for the vegetation and associated fauna since they may be functionally edge. Galli et al. (1976) indicated that woods of 0.2 ha contained only bird species characteristic of forest edges. Birds characteristic of the forest interior began appearing in islands of about 0.8 ha. Foliage and stem density are greatest per unit area in the edges and canopy, and penetration of the edge into the forest can be approximated in these terms (Bruner 1977). Height of the edge foliage can be measured or estimated. Similarly, expanding the concept of edge to include the canopy, vertical thickness of the canopy layer can also be quantified. Mawson et al. (1976) developed a model using geometric shapes to quantify tree and shrub crown volumes by layers. The resultant edge-canopy volume represents the major source of cover and nesting for birds as well as the region of greatest primary production. This volume provides a meaningful indicator of avian habitat quality (MacArthur et al. 1962, MacArthur 1964, Sturman 1968) since the remainder of the mesic forest interior is essentially open space.

Conclusions

The richness of woody species in isolated woodlots is largely a function of disturbance, whether natural or human-induced. Heavy human usage of the urban islands maintains a continual state of disturbance resulting in an increased edge effect and a high species richness from colonization of less tolerant species. Human disturbance maintains species richness near the regional peak (Loucks 1970) and, in agreement with Suhrweir

(1976), retards the island's transition to more mesic species. In rural areas, where islands are under less human pressure and disturbances are more random, an island can redevelop successionally resulting in more frequent extinction of intolerant species and a lower overall species richness in the mesic interior.

The classical species-area relationship was shown to be incapable of predicting the number of woody plant species as a function of island size for these southern mesic forests. Limits were placed on the function by (1) the finite number of woody plant species in the region, and (2) mortality of shade intolerant species under the low light levels and mesic conditions of undisturbed interiors of large woodlots. Lag in community response to earlier disturbance, size reduction, and isolation of islands obscured direct correlation.

Species richness for trees and woody plants generally increased with island size to approximately 2.3 ha. Islands smaller than 2.3 ha functioned essentially as edge communities composed of a mix of intolerant and residual tolerant species. Islands larger than 2.3 ha showed a general decline in species richness as interior, mesic conditions became established with only tolerant species persisting. Species richness ceased to decline at approximately 3.8 ha, suggesting that only the shade-tolerant, mesophytic species remained.

White ash is a vigorous, opportunistic competitor in the forest islands of metropolitan Milwaukee that responds to disturbance. It appears to be replacing the elms (*Ulmus* spp.) and may be considered a major community component of all structural strata of the southern mesic forest.

Sugar maple seedling densities were often lower in the urban and heavily disturbed sites while white ash reached somewhat higher densities. Locally heavy rabbit browsing and seedbeds unsuitable for sugar maple have been suggested to account for its low numbers. Further investigation of this relationship is needed as it has a direct bearing on the successional dynamics and future composition of the urban forest.

Community development, viewed as a series of extinctions and colonizations, is a function of the distance to the seed source of each component species. Encouraging the use of local ecotypes of upland trees and shrubs as street and yard plantings in the urban system could help to reduce interstand distance by providing seed sources. In rural areas, the retention of fencerows and other environmental corridors could provide the much-needed "stepping stones" for dispersal.

Management priorities must include protecting the large (> 4 ha), less disturbed woodlots as only they have the potential to provide self-perpetuating examples of the once regional southern mesic environment. The larger islands also function as refugia for the rarer species requiring the southern mesic habitat.

The notion of obtaining maximum species diversity in the landscape is much in vogue. The mesic forest is the terminal association, but is characterized by a relatively low species diversity. A management strategy that would preserve maximum species diversity would maintain a high proportion of edge through frequent disturbance. Diamond (1973) warns ". . . the smaller the tract, the more rapidly will forest species tend to disappear and be replaced by the widespread second-growth species that least need protection." A more rational approach would maintain forested islands large enough to support the region's stable natural community. Or, as Usher (1979) suggests, ". . . manage a few reserves that approximate to the normal species-area relation for that region since . . . they are more 'typical' than a selection of particularly species-rich sites."

Nevertheless, retention of the smaller islands and fencerows is desirable as they harbor a diverse mix of exotic, pioneer and terminal plant community components. In agreement with Forman et al. (1976), the smaller areas function as "stepping stones" from which species can be reintroduced when community equilibrium is disturbed (Sullivan and Shaffer 1975).

A top priority should include research programs and management strategies for American beech (*Fagus grandifolia*) and other species with specialized or low dispersal potential. Once eliminated from an island, natural reestablishment is not possible. The small populations of beech found in some of the Milwaukee County Parks are presently in danger of local extinction.

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